A most unusual barrens: Complex interactions between lobsters, sea urchins and algae facilitates spread of an exotic kelp in eastern Tasmania

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ABSTRACT: Sea urchin (*Heliocidaris erythrogramma*) 'barrens' in central eastern Tasmania differ from typical barrens elsewhere in that they seasonally support dense cover of the introduced kelp *Undaria pinnatifida*. Sporophytes of this kelp establish in dense stands only when the native algal canopy is reduced, and experimental removal of native algae results in greatly increased cover of *U. pinnatifida* and sediment. Urchin barrens are integral to widespread establishment of *U. pinnatifida* because urchin grazing and sediment on barrens prevents native canopy-forming algae from colonizing, but is insufficient to prevent proliferation of *U. pinnatifida*. Estimates of population growth of the urchin and *in situ* rates of lobster predation on urchins reveal that fishing of lobsters can account for increases in urchin densities, ostensibly to levels enabling barrens formation. Lobsters are far more important predators of *H. erythrogramma* than are fishes. Thus, fishing of rock lobsters may ultimately account for the proliferation of *U. pinnatifida* in this area.

1 INTRODUCTION

Two of the most critical challenges to the integrity of the structure and dynamics of nearshore marine communities are introduced species (Carlton 1999, Bax et al. 2001) and ecosystem effects of fishing in which the indirect effects of fishing a particular target species concatenate through several interaction linkages in a community (e.g. Estes et al. 1998, Mayfield and Branch 2000, Jackson et al. 2001, Steneck et al. 2002). However, these two kinds of impacts are usually considered separately. While it is widely acknowledged that disturbances and other changes to community dynamics may facilitate invasions (Lodge 1993, Parker et al. 1999), and is it recognized that fishing may alter community dynamics (Tegner & Dayton 2000, Jackson et al. 2001), the question of whether fishing may alter community dynamics to facilitate invasion of exotics has not received attention.

In this paper we review recent investigations of the invasion processes of the introduced Asian kelp (*Undaria pinnatifida*) in Tasmania. Sporophytes of this winter annual seasonally form dense, virtually monospecific, stands on sea urchin (*Heliocidaris erythrogramma*) 'barrens'. The sea urchin barrens are the single most important habitat for the establishment of dense stands of the kelp. Thus, fundamental to understanding invasion of *U. pinnatifida* in Tasmania is the need to identify the mechanism underpinning overgrazing of native macroalgae by *H. erythrogramma*.

2 UNDARIA PINNATIFIDA – PATTERNS OF OCCURENCE

Undaria pinnatifida is a large brown alga (O. Laminariales) native to the warm temperate coasts of Asia, but which has now spread to the Atlantic and Mediterranean coasts of Europe (Castric-Fey et al. 1993, Fletcher and Manfredi 1995, Curiel et al. 1998), and in the southern hemisphere to Argentina (Casa and Piriz 1996), New Zealand (Hay and Luckens 1987) and Australia. In Australia, the plant was first detected in Tasmania in 1988 (Sanderson 1990), and has now spread and established on shallow rocky reefs and cobble bottoms over several hundred kilometers of the eastern coastline of Tasmania.

Of crucial importance to inform management responses to the introduction of this species, are the processes that underpin its invasion. Despite results of experimental studies in France indicating that native canopy species resist invasion by *U. pinnatifida* (Floc'h et al. 1996), concern has been expressed that *U. pinnatifida* is able to invade by actively displacing native species (Rueness 1989, Fletcher and Manfredi, 1995). In Tasmania this concern arises in part from casual observation that areas which previously supported diverse beds of native macroalgae are now characterized by dense stands of *U. pinnatifida*.

Based on quantitative surveys at three sites in Mercury Passage in 1999 (Fig. 1) we developed the alternative hypothesis that *U. pinnatifida* is only able

to invade and establish at high densities when disturbance removes native algae. We define disturbance as any exogenous mechanism causing direct loss of algal biomass (see Chapman & Johnson 1990). At two of the three sites, sea urchin (*Heliocidaris erythrogramma*) barrens occur alongside dense stands of native macroalgae. Across all these sites it is clear that *U. pinnatifida* densities are highest on the urchin barrens, where densities of native macroalgae are lowest (Fig. 2). Although the mean density of sea urchins on the barrens (7.08 m^{-2}±SE=0.42, n=90) is relatively low, it is significantly greater than that in adjacent stands of macroalgae (0.12 m^{-2}±SE=0.17, n = 135); nested ANOVA (transformation=$\sqrt{Y}$) indicated significant differences among habitat types (native algal bed *vs*. urchin barrens, $F_{1,1}$=999.9, P=0.020) and among subsites within site/habitat combinations ($F_{8,168}$=2.54, P=0.012). In line with sea urchin barrens elsewhere, mean and modal size of *H. erythrogramma* on barrens is significantly smaller than in adjacent macroalgal beds (Fig. 3), and animals from barrens have significantly smaller gonad indices than those in adjacent algal beds (gonad index = gonad fresh weight / total fresh weight; 5.97% ±SE=0.25, n=100, in barrens *vs*. 8.98% ±SE=0.41, n=119 in algal beds; t_{194}=-6.195, p<0.0001; data collected November 1999 prior to spawning).

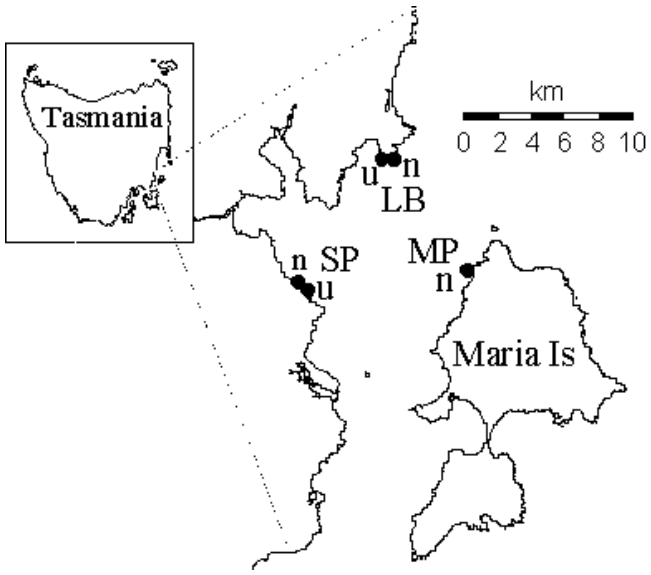
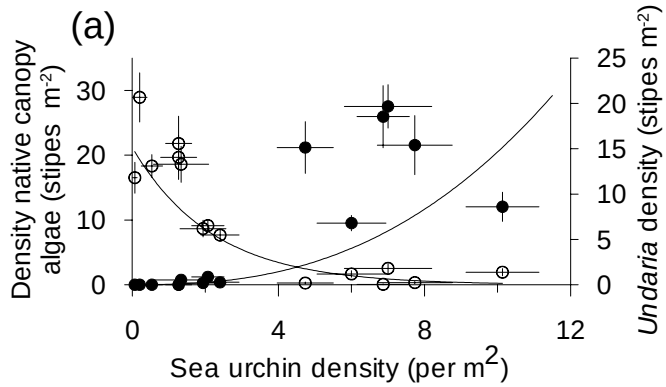


Figure 1. Study areas in Mercury Passage, eastern Tasmania. LB=Lords Bluff, SP=Stapelton Pt, MP=Magistrates Pt. 'u' = sea urchin barren, 'n' = native algal bed (n). For the basic descriptive work (presented in Figs 2,3) there were 3 subsites at each site and algae and sea urchins were enumerated in 15 quadrats in each subsite.



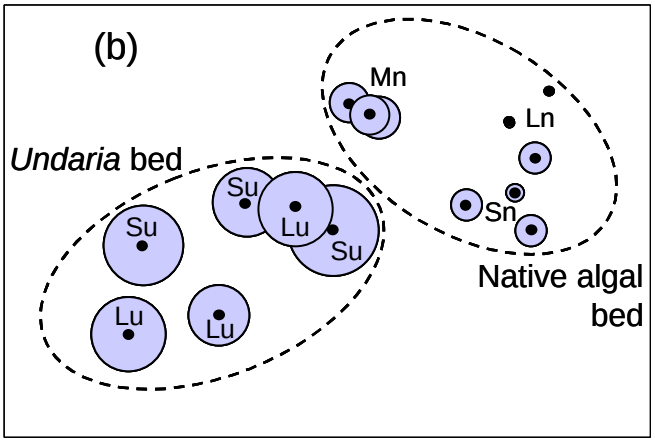


Figure 2. (a) Relationship between stipe densities of native algae (open circles, left *y*-axis), *U. pinnatifida* (solid circles, right *y*-axis) and density of *H. erythrogramma* at the 5 sites shown in Fig 1. Each data point represents the mean ±SE of a single subsite (n = 15 x 1m^2 quadrats). (b) non-metric multidimensional scaling plot of macroalgal community structure at each site and subsite overlain with sea urchin density (shaded circles) showing clearly that *U. pinnatifida* and native algal beds separate clearly on the basis of sea urchin density. (Ordination is on Bray Curtis matrix of 4^{th}-root transformed data; stress=0.07; 15 random quadrats per subsite, quadrats = 1 m^2 for sea urchin and stipe counts of larger macroalgae, quadrats = 0.125 m^2 for percentage cover of filamentous species).

While *H. erythrogramma* barrens is the most widespread habitat in this area supporting dense stands of *U. pinnatifida*, the alga is also observed at high densities in other habitat types in Mercury Passage in which the frequency and/or intensity of disturbance is high. These habitat types include unstable substrata comprised of shells, pebbles or small cobble, and at the lower boundaries of rocky reefs subject to sand scour.

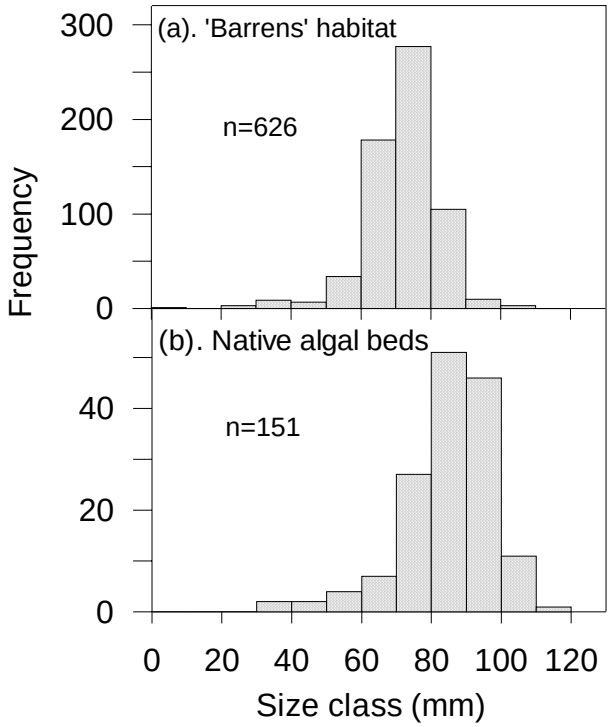


Figure 3. Size frequency distributions of *H. erythrogramma* from (a) barrens habitat and (b) native algal beds in Mercury Passage (sites in Fig. 1). Sea urchins in barrens habitat are significantly smaller than those in adjacent algal beds (Kolmogorov Smirnov, KSa=5.99, P<0.0001). Sea urchins were sampled from 90 x 1m^2 random quadrats on barrens and 135 x 1 m^2 quadrats in algal beds.

3 UNDARIA PINNATIFIDA – RESPONSE TO DISTURBANCE

To test the hypothesis that *U. pinnatifida* is only able to establish at high densities when disturbance limits cover of native algae, Valentine & Johnson (2003) conducted identical experiments at two sites in the vicinity of Lords Bluff (Fig 1). At each site the response of *U. pinnatifida* to treatments involving all combinations of ± native canopy algae and ± enhanced spore inoculum of *U. pinnatifida* was followed over 2 years (each treatment plot = 16 m^2, 3 replicate plots per treatment). Removals of native canopy algae were undertaken in spring at the peak time of spore release by *U. pinnatifida* and in winter at the beginning of the growth period of the sporophytes. No understorey algae were removed.

U. pinnatifida responded strongly in plots where native canopy algae were removed, but remained at low background levels in plots in which the canopy of native species was intact (Fig 4). A greater number of *U. pinnatifida* sporophytes developed in plots cleared in winter at the start of the sporophyte growth season than in plots where the canopy had been removed in the previous spring (Fig 4).

A similar response in the proliferation of *U. pinnatifida* sporophytes was subsequently observed in patches where the native alga *Phyllospora comosa* suffered extensive natural dieback, ostensibly as a result of localized warming (Table 1). Notably, in the experiments there was no effect of an enhanced inoculum of *U. pinnatifida* spores, reflecting that in plots without added spores there were sufficient densities of gametophytes for dense growth of sporophytes once the canopy was removed.

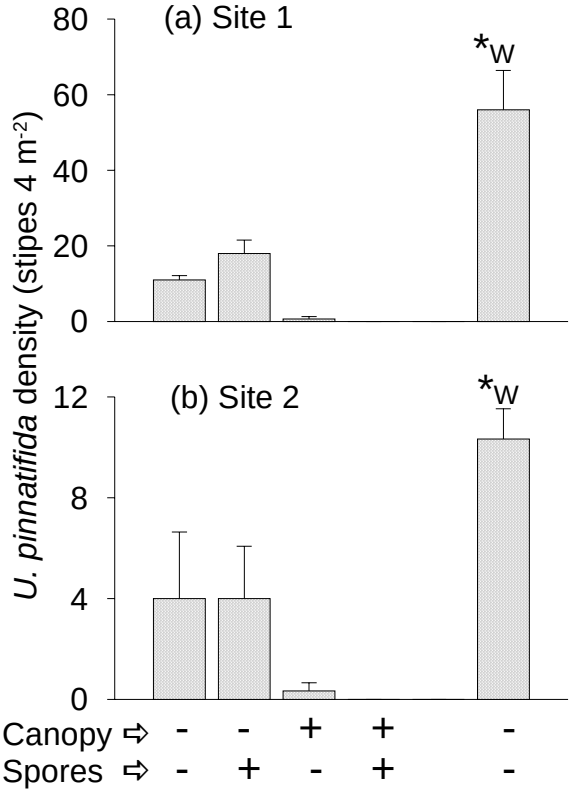


Figure 4. Response of *U. pinnatifida* to manipulations of native canopy algae ('-'=removed, '+'=canopy intact) and spore enhancement ('-'= no added *U. pinnatifida* spores, '+' = enhanced spore inoculum) 12 months after initial canopy removals. Initial canopy removals were in spring at the time of peak spore production. *W indicates treatments in which canopy algae were removed in the following winter, just prior to the growth season of the *U. pinnatifida* sporophytes. After Valentine & Johnson (2004).

Table 1. Response of *U. pinnatifida* to dieback of *Phyllospora comosa* at Lords Bluff in early 2001. Data are mean stipe densities in 16 m^2 'dieback' plots (=DP; 6-10 m depth) and in two kinds of control plots in which no dieback was observed, *viz.* shallower plots (5-6 m) dominated by *P. comosa* (=SP), and plots (6-10 m) dominated by other native canopy-forming algae (=NP) (n=6 replicates of each plot type) (after Valentine & Johnson 2004).

	stipe density (no. m^{-2} [SE])		
	Undaria	*Phyllospora*	other native algae
pre-dieback (DP)	0 (0)	34.7 (2.4)	9.2 (1.74)
post dieback			
DP (dieback)	27.0 (8.0)	1.3 (0.4)	3.8 (1.2)
SP (no dieback)	0.2 (0.2)	27.3 (2.8)	7.5 (2.0)
NP (no dieback)	1.3 (0.7)	1.3 (0.4)	32.0 (2.1)

Poor competitive ability of *U. pinnatifida* is also indicated by recovery of cover of native canopy-forming species within two years of canopy removal (Fig. 5). This recovery occurred despite significant accumulation of a matrix of sediment and filamentous algae in the removal plots (Fig 6).

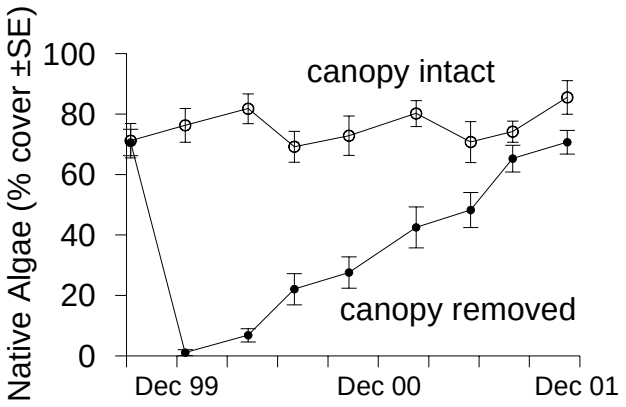


Figure 5. Recovery of native algal cover after canopy removals, compared to cover in control plots (Site 1) (After Valentine (2003).

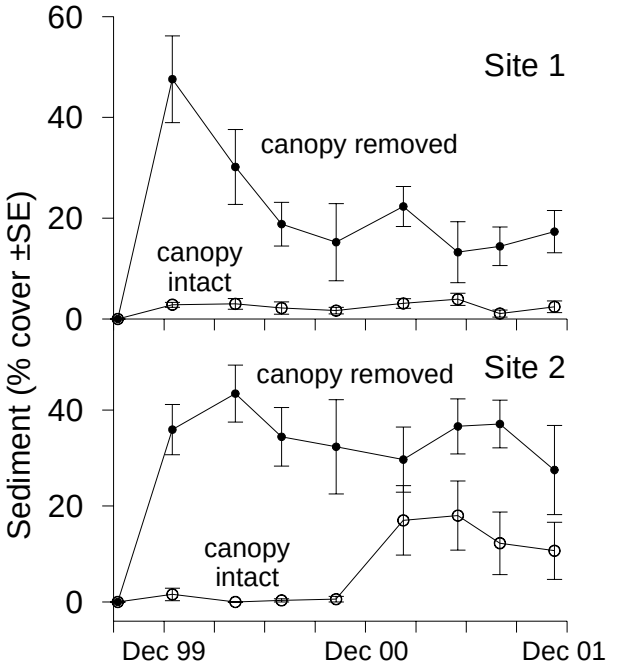


Figure 6. Cover of matrix of sediment and filamentous algae in plots from which the canopy of native algae was removed compared to sediment cover in control plots. After Valentine (2003).

These results show clearly that, at least in central eastern Tasmania, there is little evidence to suggest that *U. pinnatifida* is able to competitively displace native species, despite that gametophytes of *U. pinnatifida* are apparently well established on shallow rocky reefs. Rather, it appears that development of *U. pinnatifida* sporophytes occurs opportunistically at sites where disturbance reduces cover of native canopy-forming species. Valentine & Johnson (2003) conclude that the most widespread habitat type in Mercury Passage where disturbance has virtually eliminated native macroalgae and allow proliferation of *U. pinnatifida* is on *H. erythrogramma* barrens.

4 MECHANISMS UNDERPINNING SEA URCHIN 'BARRENS' FORMATION – ROLE OF PREDATION BY ROCK LOBSTERS

Because *U. pinnatifida* appears to 'track' disturbance events, depending on the genesis of mechanisms to reduce cover of native algae, managing the spread of this exotic kelp might be most effective by managing disturbance rather than targeting the kelp directly (Valentine & Johnson 2003). Since *H. erythrogramma* barrens are the most important habitat type for establishment of *U. pinnatifida*, understanding the mechanism(s) of barrens formation is critical in identifying potential management options.

Pederson and Johnson (in revision) tested the hypotheses that southern rock lobster (*Jasus edwardsii*) and/or reef-associated demersal fishes are important predators of *H. erythrogramma*, and that fishing of these predators can allow sea urchin populations to expand to the point where formation of barrens habitat is likely. Several lines of evidence suggested that lobsters are more important as predators of *H. erythrogramma* than are fishes. In initial experiments conducted in two regions on the east coast (Mercury Passage and the Derwent Estuary), the mortality rate of tethered sea urchins was much higher in marine reserves where predators were abundant (Fig. 7, Pederson 2003). In these experiments both fish (wrasses) and lobsters were observed to prey on tethered urchins, but characteristics of urchin remains suggested that lobsters were more important than fishes. We observed that lobster predation typically leaves most of the test intact but removes the jaws and the oral test plates, while fish predation fragments the test but the lantern is usually intact. These experiments provide an index of relative predation potential on urchins prevented from seeking shelter and escaping from predators.

This initial indication of the relative importance of fishes and lobsters as predators of *H. erythrogramma* was corroborated in an *in situ* caging experiment in which the mortality of 3 size-classes of urchins exposed to different combinations of predators was monitored over 8 weeks. There were 5 treatments (comprising all combinations of ± lobsters [L] and ± fishes [F], plus a caging 'control') established in mesh cages (3x3x1 m). Manipulated lobsters were legal size (carapace length >120 mm). Cages with treatments +L-F and –L–F had enclosed mesh tops, while –L+F cages were open, and +L+F treatments used cages with partial sides and tops. Caging controls (also +L+F) were areas of reef

without cages, and mortality in these areas was compared to that in the partial cages. Results showed a significant effect of lobsters, but not fish, on urchin mortality, and there was no evidence of a lobster*fish interaction or caging effects (Table 2; Pederson & Johnson in revision). Medium-sized adult sea urchins were most vulnerable to predation since small individuals largely remained within microhabitats offering protection from predators (e.g. in crevices and under boulders) while larger animals attain at least a partial refuge in size (Pederson & Johnson in revision). Medium-sized adult urchins were 4 times more likely to die in the experiment than their larger conspecifics (logistic model, χ^2=5.05, df=1, P=0.025).

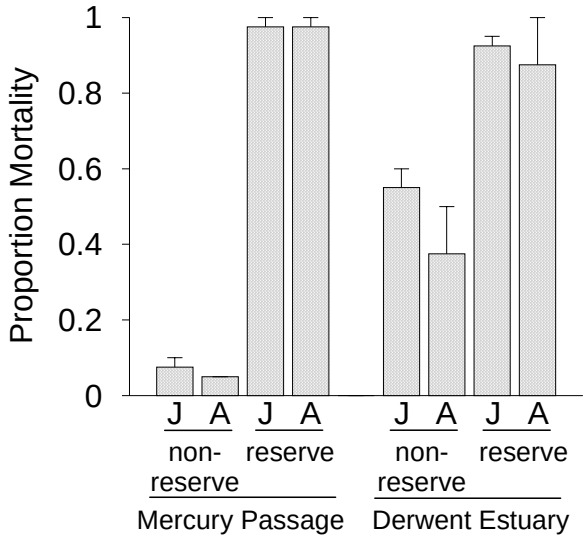


Figure 7. Mortality of juvenile (=J; 40-60 mm test diam) and adult (=A; 65-80 mm diam) tethered *H. erythrogramma* over 14 days inside and outside two marine reserves. At each site 25 urchins of each size class were tethered along each of two transects, thus data are means (+SE) of n=2 transects. After Pederson & Johnson (in revision).

Table 2. Survivorship over 8 weeks of *H. erythrogramma* subject to predation by rock lobsters and reef-associated demersal fishes. There were initially 5 sea urchins of each size class in each experimental area. Urchins ≤60 mm test diam are juveniles. Treatments are combinations of ± lobsters (L) and ± fishes (F). Data are means (SE) of n=3 independent replicates of each treatment. After Pederson & Johnson (in revision).

Sea urchin size class (test diam)	Predator Treatment				
	Control (+L+F)	-L-F	-L+F	+L-F	+L+F
40-60 mm	5.0(0)	5.0(0)	4.6(0.3)	5.0(0)	5.0(0)
61-80 mm	4.3(0.3)	5.0(0)	4.6(0.3)	0.6(0.6)	3.3(0.3)
81-100 mm	4.0(0)	5.0(0)	2.6(1.2)	2.3(0.6)	4.3(0.3)

A key issue in ecology is whether results from small-scale experiments can be scaled linearly and extrapolated to larger scales (Wiens 1989, Levins 1992). If the results from the experiments just described and others (see Pederson & Johnson, in revision) underpin larger scale patterns in species associations and ecosystem structure, then it would be expected that at larger scales there might be a stronger negative relationship between abundances of rock lobsters and *H. erythrogramma* than between demersal reef fish and the urchin. The results of large scale surveys along several 100 km of coastline indicate that this is indeed the case (Fig. 8a,b). The negative 'factor ceiling' relationship between urchins and lobsters (Fig. 8a) suggests that lobster density defines an upper limit to urchin population density.

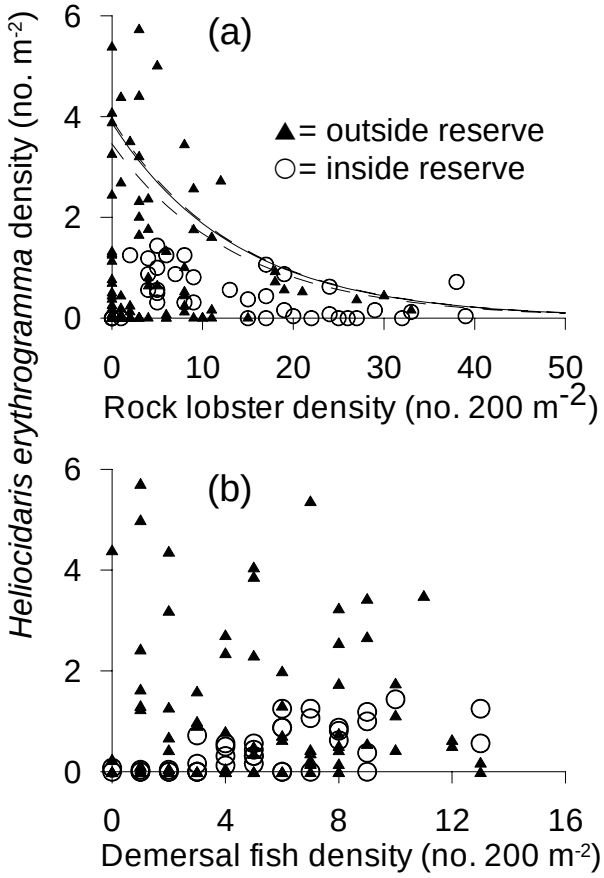


Figure 8. Surveys over large scales indicate strong relationships between sea urchin density and (a) rock lobsters, but not between urchins and (b) reef-associated fishes. Each data point is based on a 4x50 m belt transect, reflecting either the density of urchins in a 16 m^2 quadrat sampled randomly along the transect, or total counts of lobsters in each transect, or counts of fishes from swimming the entire transect. Fitted line in (a) is determined from quantile regression (95th quantile ± 95% CI; log(y) = -0.32x + 0.59; P<0.001). After Pederson (2003).

A critical issue is whether fishing of predators of *H. erythrogramma* is likely to affect urchin population densities or size structure, since demonstration of predation does not necessarily infer that predation mortality has a significant effect on population dynamics. To address this question, Pederson (2003) developed a population model of *H. erythrogramma* and compared predicted densities of populations

subject to the different levels of predation mortality observed inside and outside reserves. The model was based on age-specific growth and mortality and the age-frequency distribution estimated in Mercury Passage. Results indicate asymptotic urchin densities of <4 m^{-2} at predator levels found in unfished marine reserves, and ca. 10 m^{-2} in fished areas where predation mortality is reduced. Notably, these barrens are maintained at densities >7-8 m^{-2}. The model indicated that several plausible recruitment scenarios would realize sea urchin populations at densities >10 m^{-2}. While commercial sea-urchin divers have provided individual histories of their direct observations of destructive grazing of macroalgae by the sea urchins, the densities of sea urchins necessary to create barrens have not been recorded. Our observations of sea urchin feeding aggregations indicate that densities of the order of 40 m^{-2} are likely to be sufficient for barrens formation. If so, then this would require animals from 4 m^2 of reef to aggregate into 1 m^2. Notably, analysis of age-frequency distributions did not suggest that present densities of sea urchins were the result of a single prodigious recruitment event (Pederson 2003). We conclude that fishing of sea urchin predators on the east coast of Tasmania, and of rock lobsters in particular, is sufficient to account for *H. erythrogramma* densities building to the point where destructive grazing of macroalgae can commence.

5 SYNTHESIS

5.1 *Complex interactions link fishing and establishment of introduced U. pinnatifida*

Our experiments and observations reveal a complex suite of interactions that manifest ultimately as *H. erythrogramma* barrens providing a unique habitat facilitating proliferation of the introduced kelp *U. pinnatifida*. The finding that establishment of sporophytes of *U. pinnatifida* at high densities, and continued maintenance of dense stands of the alga, depends fundamentally on mechanisms to reduce cover of native canopy-forming species is consistent with results of experiments with this species (Floc'h et al. 1996) and other exotic large brown algae (Andrew and Viejo 1998) in Europe. There is no evidence in Tasmania that this kelp is able to competitively displace native species, as has been previously suggested (Rueness 1989, Fletcher & Manfredi 1995). This opportunistic behaviour is consistent with its life history characteristics of an annual habit, high growth rates, and large reproductive output.

In responding to concerns about establishment of dense monospecific stands of *U. pinnatifida*, it is clear that *H. erythrogramma* barrens are the key habitat in this region, and therefore that mechanisms determining the extent of sea urchin barrens are of fundamental importance. There are insufficient baseline data to provide a quantitative historical perspective of the extent of *H. erythrogramma* barrens in Tasmania, how anectodal evidence from divers suggests that barrens formation is a recent event of the past 3-4 decades. It is unambiguous that predation on *H. erythrogramma* in marine reserves, where predator densities are much elevated relative to areas open to fishing (Edgar & Barrett 1999), is significantly greater than in equivalent areas outside protected areas. The evidence reviewed here suggests that most of this predation mortality is attributable to rock lobsters (*J. edwardsii*). Population models suggest that the observed reduction in predation mortality associated with fishing urchin predators realises significant increases in *H. erythrogramma* densities, ostensibly to levels sufficient for destructive grazing of macroalgae (Pederson 2003). Not surprisingly, long-term monitoring in the Maria Is marine reserve has revealed significant declines in *H. erythrogramma* densities relative to control sites outside the reserve (N. Barrett, pers. comm.). These patterns in community dynamics reflect those observed in similar types of communities inside and outside marine reserves in New Zealand (Shears & Babcock 2003).

We argue that the trophic link between lobsters and *H. erythrogramma* on the east coast of Tasmania is now effectively removed, since it is only lobsters above legal size that prey significantly on *H. erythrogramma* (Pederson 2003), and the biomass of legal-sized lobsters on the east coast is greatly reduced. Over the period 1970-2002, depending on the year and region, legal-sized biomass on the east coast of Tasmania ranged between ca. 2-12%, with an average of 7.3%, of the virgin stock (Frusher et al. 1997, S. Frusher unpub data). Our recommendation is that if managers wish to reduce the likelihood of further expansion of large monospecific stands of *U. pinnatifida*, then expansion of *H. erythrogramma* barrens must be addressed, which is likely to require building biomass of legal-sized rock lobsters.

Issues of effects of fishing and introduced marine species are usually treated separately. This work is the first to show clear connections between fishing of native species and spread of exotic marine algae.

5.2 *A most unusual barrens*

Sea urchin barrens are usually characterized by the virtual absence of macroalgae (e.g. Lawrence 1975; Chapman & Johnson 1990). Clearly then, the *H. erythrogramma* barrens in central eastern Tasmania are unique in that they facilitate proliferation of *U. pinnatifida*. There are several important components to this scenario. First, urchin densities are notably lower than is typical of barrens elsewhere in the world (e.g. see Lawrence 1975, Bernstein et al. 1981, Estes & Duggins 1995). This does not mean

that *U. pinnatifida* is immune from urchin grazing since, on the barrens, sporophyte densities are routinely lower in control plots containing sea urchins than in plots from which urchins are removed (Fig 9). Indeed, existence of *U. pinnatifida* sporophytes on barrens is precarious, since depending on the balance of urchin densities and behaviour, and recruitment rates of the alga, in some years very few sporophytes may develop (Fig. 9). However, in most years urchin grazing is insufficient to prevent sporophyte development.

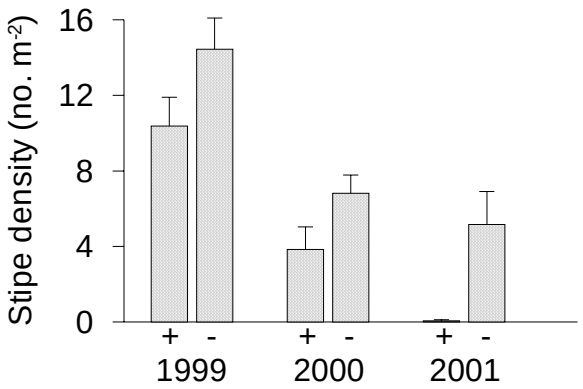


Figure 9. Density of *U. pinnatifida* in 16 m^2 treatment plots with (+) and without (-) sea urchins on barrens at Lords Bluff. Data are means +SE. After Valentine & Johnson (in revision).

A second feature is that it is not only urchin grazing that prevents native canopy-forming species from establishing on these 'barrens'. In a large experiment on urchin barrens at Lords Bluff, Valentine & Johnson (in revision) examined responses of algae to eight treatments involving all possible combinations of ± sea urchins, ± *U. pinnatifida*, and ± enhanced spore inoculum of native canopy-forming species. Despite that this area had once supported extensive macroalgal cover, no visible canopy-forming species developed in any treatment over 2.5 years, even in plots subject to spore enhancement and from which sea urchins and *U. pinnatifida* were removed. This surprising result may reflect that development of a matrix of sediment and filamentous algae over these areas, as occurred in the smaller scale 'canopy removal' experiment (Fig. 6), is sufficient to inhibit establishment of macroalgae, as has been reported elsewhere (e.g. Devinny & Volse 1978, Kendrick 1991, Umar et al. 1998). However we note that sediment accumulation in the small scale experiment did not prevent recovery of canopy-forming species (Fig. 5). This contrast may indicate either non-linear effects in scaling up from small experimental plots to extensive areas of barrens, or that cover of the sediment matrix on the urchin barrens was more extensive (mean cover ranged from 33-59% depending on treatment, with an overall mean of 50.5% cover) than in the removal plots in the macroalgal bed (see Fig. 6).

The overall conclusion is that once these urchin barrens form they represent a stable configuration (persistence stability, *sensu* Johnson & Mann 1988) that facilitates establishment of *U. pinnatifida* but not native canopy-forming species. Removal of the species that characterise this configuration (i.e. the sea urchins and *U. pinnatifida*) is not sufficient to return the community to a diverse assemblage of native macrolagae.

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